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being essentially a synaptic system. It would appear that that primitive type of nervous organization predominantly present in such coelenterates as the sea-anemones, but preserved in vertebrates only among certain autonomous internal organs,[5] still forms in molluscs a highly important feature of the animal's action system.[8]

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[1] Contributions from the Bermuda Biological Station for Research, No. 113.

[2] Crozier, W. J., and Arey, L. B., "Sensory reactions of Chromodoris zebra," *J. Exper. Zoöl., Phila.*, (in press).

[3] Crozier, W. J., 1919, *J. Gen. Physiol., Baltimore*, **1**, No. 6.

[4] For more detailed treatment of the complex conditions here entering, consult papers cited in footnotes two and three.

[5] cf. Parker, G. H., 1919. *The Elementary Nervous System.* (Philadelphia.)

[6] Frölich (*Zs. Allgem. Physiol., Jena*, **11**, 1910, p. 269) had already demonstrated that in *Aplysia* the site of action of strychnine is the 'cerebral' ganglion.

[7] Cushny (*Quart. J. Exp. Physiol., London*, **12**, 1919, p. 153) points out that the depression of the reflex thresholds, rather than, as often held, the conversion of 'inhibition' to 'activation' (where reciprocal innervation is involved), is the essential feature of the strychnine effect.

[8] This conception of the nervous organization of *Chromodoris* agrees with the opinion held by Bethe respecting *Aplysia*, but the evidence here relied on is much more complete (cf. Bethe, *Allgem. Anat. u. Physiol. d. Nervensystems*, Leipzig, 1903).

ARE GENES LINEAR OR NON-LINEAR IN ARRANGEMENT?

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Communicated, August 13, 1919

As to the question whether the genes in a linkage system are linear or non-linear in arrangement, Morgan and his associates[1] still maintain their former view that the arrangement is strictly linear. I have questioned the validity of this view on the following grounds.[2] (1) The forces which link the genes together are possibly molecular rather than mechanical. If so, it is doubtful whether the entire system consists of a simple thread-like chain. (2) Construction of a model in three dimensions of the relations of the genes in the sex chromosome of *Drosphila ampelophila* as shown by the data of Morgan and Bridges,[3] and on their own assumption that distances are proportional to cross-over values, proves that the arrangement can not be linear. A similar reconstruction for the sex-linked genes of *D. virilis* shows the same thing for that species even more emphatically. (3) The linear hypothesis makes necessary the further assumption that cross-overs greater than 50% occur within the linkage system.

Such values have not been observed and are logically impossible. (4) The hypothesis of non-linear arrangement is simpler because it eliminates secondary hypotheses needed on the linear hypothesis to harmonize greater with lesser cross-over values, particularly the hypothesis of double crossing-over.

Point (1) is dismissed by Morgan and his associates with the remark that it is "probably not intended to be taken seriously." I, therefore, renew the suggestion and invite "serious" consideration of it. They argue that chromosomes are thread-like and that accordingly linkage-systems must be thread-like. This seems to me unconvincing, because we do not know how much of the visible chromosomes is composed of genes and how much is something else. Further it may be that the genes are not *in* the chromosomes at all but merely *attached* to them, especially if the attachments are molecular rather than mechanical. All the observational facts concerning linked genes would be equally well satisfied by such a view. It should be borne in mind that we have no evidence whatever that the chromosomes *are* genes but only that the genes are in some way connected with them. Accordingly the spatial relations of genes can not be legitimately inferred from the shape of the chromosomes.

Against point (2) the chief attack of Morgan and his associates is directed. No objection is made to the method employed of reconstruction in three dimensions, but the reliability of the data used is repeatedly assailed. Now the data consisted of Table 65 of Morgan and Bridges on which the authors based their Diagram I showing the arrangement of the genes as linear. Surely this same data could legitimately be used in testing the hypothesis that the arrangement is non-linear. Moreover the Table 65 is, so far as I know, the *only* table in which the authors have ever given a comprehensive summary of their data. At the head of the table, they say "In Table 65 all data so far secured upon the sex-linked characters are summarized." Now my model, based on actual measurements of distances indicated by Table 65, showed conclusively that the arrangement of the genes can not possibly be linear. No alternative is therefore left to Morgan and his associates except either to repudiate their Diagram I or to repudiate the data on which that diagram was ostensibly based. They choose the latter alternative. In discussing the relation to each other of any three genes, they now reject all data except such as are based on simultaneous observation of all three loci. This is done for the seemingly good reason that in this way all disturbing agencies are eliminated, such as differences of temperature, age, or associated genes. But by so doing, they introduce other and much more serious disturbing agencies.

Take the case of the three genes, yellow, white and bifid, which both they and I have singled out as well illustrating the merits of our respective methods. Morgan and Bridges[3] in describing their method of constructing 'Diagram I' say. "Thus if the experiments give a cross-over value of 5 per cent for white and bifid, we say that white and bifid lie 5 units apart in the X chromosome. Other experiments show that yellow and white are about 1 unit apart, and that yellow and bifid are about 6 units apart. We can therefore construct a diagram with yellow as the zero, with white at 1, and with bifid at 6." But the Table 65 of this same publication, on the basis of which, it is explicitely stated, Diagram I was constructed, gives these distances more exactly as yellow-white, 1.1; white-bifid, 5.3; yellow-bifid, 5.5. The authors in the passage quoted ignore a considerable discrepancy with these figures, since it is obvious that if the three genes are, as supposed, in a straight line, the distance yellow-bifid should equal the sum of yellow-white plus white-bifid, or 6.4 (instead of 5.5). Commenting on the actual observations in the case, I said, "Therefore bifid can lie neither above nor below yellow and white, in the line which joins them, but must lie laterally about equidistant from both." Returning to the case, Sturtevant, Bridges and Morgan now reject all but a small part of their previous data, retaining only two experiments in which all three loci were simultaneously under observation. The changed character of the data is shown in Table 1. Yellow-white is not materially affected but white-bifid is now 3.5, instead of 5.3, and yellow-bifid is 4.7, instead of 5.5. Are the new values more reliable than the old ones? So far as amount of data is concerned, they are much more liable to error through random sampling. If disturbing agencies are at work in isolated experiments, their effect is less likely to be felt in larger totals based on experi-

TABLE 1

	FULL DATA		SELECTED DATA	
	Cross-over values	Cases	Cross-over values	Cases
Yellow-white	1.1	81,299	1.2	1,218
White-bifid	5.3	23,595	3.5	1,218
Yellow-bifid	5.5	3,681	4.7	1,218

ments made under varied conditions. On this general ground the full data would seem to be preferable to the selected data. But let us, for the sake of argument, accept the smaller amount of selected data. What are the observational facts? In a total of 1218 flies, the gene yellow was observed to separate from the other two genes in 15 cases, and bifid was observed to separate from the other two genes in 43 cases, but white was not observed to separate from the other two genes. The 15 cases, in which yellow separates, make up 1.2% of the total, which is put down as the cross-over value between yellow and white, but in reality it is the cross-over value between yellow on one hand and the group white-bifid on the other hand. Likewise the 43 cases, which form 3.5% of the total, are put down as the cross-over value between white and bifid, but in reality they represent the cross-overs between bifid on one hand and the group yellow-white on the other. It is not certain that white with yellow attached would show the same percentage of cross-overs as without yellow attached. Indeed, in their doctrine of *interference*, the authors have long held that it would not. According to that doctrine, in case a break occurs between yellow and white, there is no chance whatever that a break will occur simultaneously in the near-by region between white and bifid, and *vice versa*, if a break occurs between bifid and white, there is no chance that a break will occur also between yellow and white. Accordingly in calculating the percentage of cross-overs for yellow-white, 15 should be deducted from the total number of cases, and in calculating the percentage of cross-overs for white-bifid, 43 should be deducted from the total, *if the principle of interference is valid.* Such correction would increase slightly the cross-over values for yellow-white and yellow-bifid, whose sum would now exceed the cross-over value given for yellow-bifid, 4.7, and would again put the three genes out of line.

It appears, then, that the authors have failed in two different attempts to establish their linear theory in the case of the three genes yellow, white and bifid. Morgan and Bridges in their equation, 'about 1' + 5 equals 'about 6,' seriously distort facts which should be very exactly stated if the linear hypothesis is to have a basis in fact as well as in fancy. The real relations, as given in their Table 65, are $1.1 + 5.3 > 5.5$. The new equation, which they now offer as a substitute for the old one, is $1.2 + 3.5 = 4.7$, which looks all right. The two halves of the equation balance, but the balance is a forced one. To obtain it two very questionable things are done. First, nearly 99% of the authoritative observations are suppressed;

secondly, the remaining observations are treated in utter disregard of the principle of 'interference' which has long been recognized by the authors and has never been repudiated by them.

But we are not without other and independent evidence of the relations between the three genes, yellow, white and bifid. Each of these has known linkage relations with other genes of the system. Pertinent facts from Table 65 of Morgan and Bridges are reproduced herewith in Table 2. They show that yellow is farther removed from vermilion, miniature and rudimentary than is either white or bifid, since the cross-over values are in every case higher. This supports Morgan's view that yellow is at the distal end of the system. If white and bifid lie in succession below yellow, white should be *farther* removed than bifid from genes lower in the system. Data are given for the distances to four such genes. In two cases (vermilion and rudimentary) white is nearer than bifid, in two other cases (miniature and forked) bifid is nearer than white. The more reliable cases, based on larger numbers, are those which place *white below bifid*, minimal observations 2724 and 899 respectively. The numbers which place bifid below white are 306 and 219, too small to carry much weight. We may conclude that so far as evidence given by table 65, Morgan and Bridges, is concerned, bifid is certainly as remote as white and probably more remote than white from the lower parts of the linkage system. If so, bifid cannot lie in line with yellow and white, below them in the linkage chain, as maintained by Morgan and his associates. This conclusion agrees with the relations shown in my model, but not with those shown in their Diagram I.

TABLE 2

	CROSS-OVER VALUES	CASES
Yellow-vermilion	34.5	13,271
Yellow-miniature	34.3	21,686
Yellow-rudimentary	42.9	2,563
Bifid-vermilion	31.1	2,724
Bifid-miniature	30.6	219
Bifid-rudimentary	42.7	899
Bifid-forked	42.5	306
White-vermilion	30.5	27,962
White-miniature	33.2	110,701
White-rudimentary	42.4	6,461
White-forked	45.7	3,664

With reference to the reconstruction for *D. virilis*, which is very clearly three-dimensional, the authors have nothing whatever to say. It would not be known that they had seen the paper[4] in which that reconstruction is described except for a footnote at the very end of their paper, which reads "Castle concluded that the white-forked value of 45.7 used by him, is somewhat too high, which is true; but there were available to him more than 40,000 flies (Bridges, *Genetics*, **1**, 1916 and Weinstein, *Ibid*, **3**, 1918) giving the lower value, in contrast to the less than 4000 flies on which the high value was based." There seems to be here a veiled rebuke that I did not look outside Table 65 of Morgan and Bridges for additional data. I saw no reason for doing so since Morgan and Bridges had based their linear diagram exclusively on "the data summarized in Table 65," and it seemed to me fair to test an alternative hypothesis by the same data. Moreover I was not at that time aware that additional cases had been recorded bearing on the white-forked linkage relation. In comparing the linkage system of *D. ampelophila* with that of *D. virilis*, I mentioned quite incidentally the longer distance recorded for the former species but that my model indicated this value to be probably too high, "since the wire joining white with forked in the model is too long to harmonize fully with other linkage values given by Morgan and Bridges, the wire being curved." If my model, merely by a curved wire, was able to detect an error which would otherwise have been overlooked by me, and which it required 40,000 additional flies to prove, the reconstruction method certainly has utility. Now I have made certain predictions as to what some undetermined linkage relationships in *D. virilis* will be found to be, based on the reconstruction figured in my former paper. An experimental test of their correctness is invited. Let us taste this pudding to prove or disprove its edibility.

With reference to point (3), Morgan and his associates consider cross-over values greater than 50 possible, though not as yet observed. They are led to this conclusion by the consideration that values greater than 50 are obtained by summation of short distances, on the hypothesis of linear arrangement. Forced to a choice between non-linear arrangement and map distances greater than 50, they choose the latter, and then contend that distances greater than 50 are possible and would actually be observed except for double crossing-over. For my part, I can not conceive of a mechanism which would tie two genes *together* in such a way that they will subsequently *separate* from each other oftener than they will remain together, yet this is what the idea of cross-overs in excess of 50 per cent amounts to.

With reference to point (4), it is admitted by Morgan and his associates that "double crossing-over has no meaning, if three genes are imagined as not lying in a straight line." It is accordingly a secondary hypothesis needed to help out the hypothesis of linear arrangement, but it can not be cited as proof of that hypothesis, which must stand or fall on its own merits. I can see no reason *a priori* why two or more breaks should not occur simultaneously in different parts of a linkage system, whether linear or non-linear, but this is no evidence that, every time a particular gene separates from two others, it has done so by two independent breaks, the view necessitated by the linear hypothesis. The relation of certain observational facts to the idea of double crossing-over is correctly stated by Plough[5] in relation to the alternative hypotheses. On a non-linear hypothesis, temperature affects "long chromosomal distances" (high cross-over values) less than small ones; on the linear hypothesis, temperature acts by changing the frequency of double crossing-over. This is no proof of either hypothesis, but a statement of fact in terms of each.

[1] Sturtevant, A. H., Bridges, C. B., and Morgan, T. H., these PROCEEDINGS, **5**, 1919, (168).

[2] Castle, W. E., these PROCEEDINGS, **5**, 1919, (25).

[3] Morgan, T. H., and Bridges, C. B., "Sex-linked inheritance in Drosophila," *Carnegie Inst., Washington Publ.*, No. 237, May 8, 1916.

[4] Castle, W. E., these PROCEEDINGS, **5**, 1919, (32).

[5] Plough, H. H., these PROCEEDINGS, **5**, 1919, (167).

ON VARIATION IN TARTARY BUCKWHEAT, FAGOPYRUM TATARICUM (L.) GAERTN.

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Introductory.—From the morpho-genetic point of view the manifestation of dimorphism in certain races of plants—the so called ever-sporting varieties—presents a very interesting problem. The remarkable feature of these races is the constancy with which the two diverging forms of the same organ are transmitted in ever-sporting fashion: no breeding method has, as yet, been conceived by which, for instance, certain variegated types of plants or certain strains of Matthiola, could be induced to breed true. These races appear as compound forms ever-transmitting the potentialities of the two component types.